DESMOGNATHUS FUSCA (RAFINESQUE) AND SPELERPES BILINEATUS (GREEN).

HARRIS H. WILDER.

As the two species which form the subject of this paper are widely distributed over the United States, it is probable that the differences in environment in the different regions may cause them to vary somewhat in their mode of life. The observations recorded here are confined to the Counties of Berkshire, Franklin, Hampshire, and Worcester, in the state of Massachusetts, and the statements made concerning their frequency, manner and times of occurrence, etc., are primarily applicable to this region. It will also be noticed that the authors quoted, with the exceptions of BAIRD and COPE, have in mind a restricted locality in each case (Massachusetts, Maine, New York) not far from the region in which these observations were made.

The object of this paper is to render available for laboratory purposes, and especially for the study of histology, two of our abundant native salamanders, which have hitherto been too much neglected, both because they are not easily found without a little experience and because they are apt to be confused with each other, especially during their larval life. The ease with which European investigators may obtain and identify their one classical species, *Salamandra maculosa*, without needing to be experts in systematic literature, or running the risk of erroneous conclusions by confusing externally similar species, is often envied here in America, where our very wealth in Urodelan material is a frequent source of vexation to the investigator, who realizes that even in histological research he cannot afford to be mistaken in the species studied. The two species considered here present many advantages which should make them favorite animals for laboratory research, when the

difficulties of finding them and distinguishing them from each other are once removed.

Early Reports of their Occurrence. — The earlier writers on the subject seem to have considered both species very rare, a circumstance which must be attributed wholly to their habit of concealment and the difficulty of finding them to one not familiar with their ways. They are evidently indigenous species, and we cannot here have to do with a recent increase in numbers, as in the case of the English sparrow or the periwinkle (*Littorina*). The first of these two salamanders to be discovered was *Desmognathus fusca*, first described by RAFINESQUE ('20) as *Triturus fuscus*, described later by HARLAN ('22) under the name of *Salamandra picta*, and cited as such by STORER ('37) in his "Report."

STORER states that he has never met with this species himself, but includes it in the list of Massachusetts Amphibia on the authority of Dr. PICKERING, who had seen one specimen that was found in a well in Ipswich, Mass.

DEKAY ('43) includes this species among the fauna of the state of New York, on the ground that it has been found both in Massachusetts and in Pennsylvania. The other associated species, *Spelerpes bilineatus*, does not appear to have been reported by any of the above authors, and was first described by GREEN ('18), who found it in New Jersey and named it *Salamandra bilineata*. It is thus clear that the two species in question, in spite of their abundance, were considered rare by the earlier authors.

Of especial interest to me has been a more recent report, by J. A. ALLEN ('68), on the Amphibia "found in the vicinity of Springfield, Mass.," in which he adds, after the name *Spelerpes bilineatus*, "one specimen, rare."

The next name on the list is that of *Desmognathus fusca*, which he has not found at all, but quotes it as having been found in the state. He writes that this species is "equally rare with the preceding" (*i.e.*, *S. bilineatus*). This failure to find these two commonest species is the more singular since the author proves himself a careful collector by including in his list such species as *Pseudotriton salmoneus* and *Plethodon gluti-*

nosus, which are rarely met with in this locality. It cannot be said, however, that all authors are in accord concerning the rarity of these two salamanders. It is noticeable that BAIRD ('50) and COPE ('89), both of whom had exceptional opportunity to study specimens from an extensive area, do not consider it rare. COPE ('89) distinctly states, on the other hand, that *D. fusca* is "perhaps the most abundant salamander in N. America."

Habitat. — Both of the salamanders in question are similar in habit and are commonly found associated. Although both are very common, they are so skilfully concealed, at least by day, that special knowledge is necessary in order to collect them in abundance. This is doubtless the reason why they have been considered rare.

They are found in and about running brooks that are plentifully supplied with small stones, and they seem to prefer spots shaded by trees. Perhaps the best brooks of all are the little mountain streams that run swiftly down quite steep inclines, forming miniature cascades alternating with small shallow basins. Mountainous regions abound in such brooks, which may be usually located from a distance by noting the places where the slopes of two hills converge, forming a ravine. When such a brook is found, begin the search by turning over all the stones and bits of fallen logs that lie in the immediate vicinity of the edge of the brook. Stones, lying a foot or more above the water and upon the dry bank, will yield nothing, and, on the other hand, stones nearly or wholly submerged in the flowing water will be profitless, since any animals contained beneath them may easily escape by slipping along with the turbid current. The best stones are rather irregular ones, lying on the edge of the brook, and with the bottom surface just below the level of the water. The right sort of a stone, when lifted, should reveal a shallow cavity formed in the wet sand or mud, but containing little or no water at the moment at which the stone is removed.

A little experience will enable the seeker to determine just which stones or other objects lie in the right position to serve as protection for the salamanders, and thus the labor becomes

much lessened. Since the adult salamanders are extremely slippery and often very rapid in their movements, it is advantageous to keep in one hand a small net of cheese cloth, having an aperture about six inches across, and with a very short handle.

The larvæ of both species are to be sought for in the water, and may be seen lying upon the bottom of the quiet pools, especially those with a fine gravel bottom. Even at this stage they are fond of concealment, and if there are small stones, fallen leaves, or other objects in these miniature basins, they should be removed and the water allowed to settle. The larvæ may be easily captured by means of the net. This should be laid upon the bottom and the larva driven into it by approaching it from behind with the hand or a small stick. The great majority of the larvæ collected in this way are those of *Spelerpes*, as it remains much longer in the larval state, but the very similar larvæ of *Desmognathus* occur in similar places and are very difficult to distinguish from the others. (See below.)

Adults. — As the two species belong to different subfamilies, it would seem an easy matter to distinguish the adults, but unfortunately the most distinctive characters are skeletal, and the external feature, such as color, number of costal folds, etc., although noticeably different in extreme or typical specimens, show so many gradations and intermediate forms that the determination is in many cases extremely difficult. Both species are dark above, marbled along the sides, and without pigment ventrally. Both species possess a broad dorsal stripe with crenulate edges. This stripe in typical specimen of *D. fusca* is very dark brown, so that in living specimens it merges almost indistinguishably into the dark slate color which limits it laterally. In the other species the dorsal stripe is usually light brown or fawn color, lighter at its outer edges and bordered by a very dark brown stripe, hence "*bilineatus*." It is, however, quite usual to find specimens of *D. fusca* with a light rufous dorsal band, set off very conspicuously from the slate-color at its outer edges ; while in many specimens of *S. bilineatus* the dorsal band is quite dark, without lighter edges, thus blending

into the dark lateral line which in time becomes lost in the dark color of the flanks, the result being similar to that seen in the lighter specimens of *D. fusca*. The ventral side furnishes a surer test, as it is usually of a light lemon yellow color in *S. bilineatus* and white and semi-transparent in *D. fusca*.

This yellow color of the former species changes to a light salmon pink in specimens thrown alive into aqueous corrosive sublimate. As for general shape and size, *D. fusca* attains a greater size, and in these large specimens (10 cm. +) the large muscles of the jaw form definite protuberances upon the head. *S. bilineatus* is not as robust a species as the other, and the tail particularly seems more slender and longer in proportion. The number of costal folds may often be useful as a diagnostic, but this character seems liable to individual variation, and one is always in doubt where to place the beginning and end of the series counted. In *D. fusca* there are generally twelve folds (*i.e.*, the myotomes, not the myocommata) between the fore and hind limb, while *S. bilineatus* shows usually fourteen or fifteen. These numbers can, however, be used for comparison only in a general way, for the relative position between these folds and the place of origin for the limbs appears to be subject to variation. Perhaps the surest method of distinguishing is to collect a few typical specimens of each, and use them as standards for comparison, employing the other diagnostic points as they may seem applicable in individual cases.

Eggs. — The eggs of *S. bilineatus* appear to be the more common, or at least the more usually found, and may be obtained during May and June. I have found them at the following dates: May 27, June 12. They are deposited in a single layer upon the lower side of submerged stones, each batch containing from 30–50 eggs. The stones which are suitable for this purpose must be in the form of an arch allowing the water to flow beneath, as in the diagram, Fig. 1. They are generally in the more rapidly flowing portions of the brook, but the depth of water must be such that the eggs are at all times entirely submerged, as the dash of the surface ripples striking against them would subject them to mechanical injury.

The eggs appear attached to the surface of the stone by gelatinous threads proceeding from the outer envelope, and although they are generally contiguous, they are each attached separately. Within the eggs the embryos lie free, the heavier

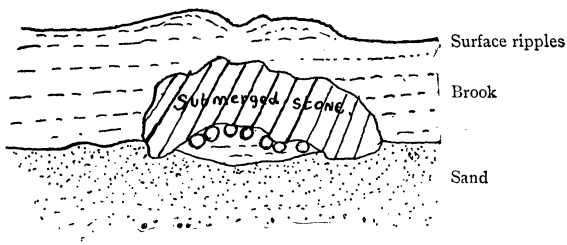


FIG. 1. — Diagram showing method of deposition of eggs employed by *Spelerpes bilineatus*.

yolk being always beneath. When the normal position is changed by the sudden overturning of the stone, the eggs roll over simultaneously in order to resume their normal position.

The eggs and their manner of deposition have been well described by VERRILL ('62, '63), although the author considers

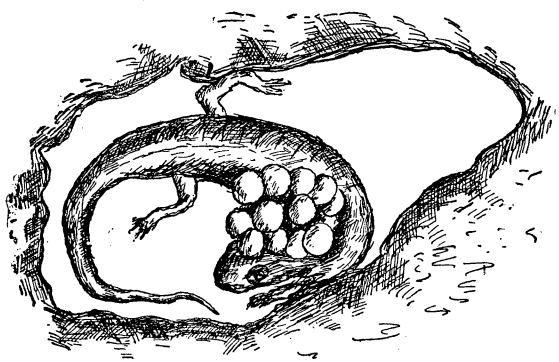


FIG. 2. — *Desmognathus fusca* ♀ with egg-rosary. Natural size.

them as the eggs of *Desmognathus fusca* and describes them under that name.

The eggs which really belong to this latter species, as described by BAIRD ('50) and later by COPE ('89), are laid in a long string and wrapped around the body of the female like a rosary. COPE'S statement is as follows: "Professor Baird originally noticed the curious disposition of the eggs in this species,

which I have verified on a few occasions. As in the Anurous genus *Alytes*, the eggs, on emission, are connected by an albuminous thread, which soon contracts and hardens. One of the sexes protects this rosary by wrapping it several times round the body and remaining concealed in a comparatively dry spot. How long this guard continues is not known." (COPE, '89, pp. 196, 197.)

After searching for such eggs during several seasons in vain, I was able finally to confirm these statements by means of a batch of eggs which were laid in my laboratory *terrarium*. When found (June 1, 1898), the position of the mother and

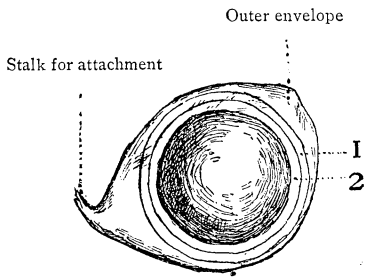


FIG. 3.

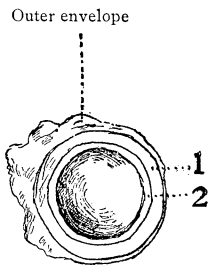


FIG. 4.

FIG. 3. — Egg of *Desmognathus fusca*. × 5.
FIG. 4. — Egg of *Spelerpes bilineatus*. × 5.

eggs was as represented in Fig. 2, which is drawn as though looked directly down upon from above.

The adult lay beneath a brick and in an irregularly oval hollow made in the mud, evidently by herself.

The eggs, which showed then no signs of development, and which must have been just laid, were, indeed, wrapped about the body of the parent, but not in a definite single string. Each was surrounded by a loose outer membrane which tapered a tone end to a strong cord, and several or all of these cords seemed to focus at a single point, much like a bunch of toy balloons held in the hand of a street vender. The attachment to the body was loose, and was evidently effected by the female by winding her body in among the strings. The eggs changed their position somewhat from day to day, as though, by the movement of the parent, new combinations had been

produced. It is even possible, in consideration of the marked nocturnal habits of this species, that the female may leave the egg-mass during the night, returning to it by day.

Comparison of the Eggs. — The comparative size of the eggs of the two species is shown in Figs. 3 and 4, in which they are drawn five times the natural size. Each appears protected by three membranes, two that fit closely and an outer loose one. It is by means of strings proceeding from this latter that the one is attached to the parent and the other to the surface of the stone, although in the latter case there appears to be a definite adhesion, in which not only the stringy processes but also the surface of the membrane itself participates. As the development shows, the egg of *Spelerpes* is holoblastic, like the more usual amphibian egg, while that of *Desmognathus* is meroblastic.

Development of Spelerpes. — Figs. 5–19 represent a series of views illustrative of the external development of *Spelerpes* and drawn to the same scale (× 5). As the eggs used in these observations were of several different ages, it was not easy for me to fix definite time-limits to the several stages.

The oldest eggs collected were almost at *Stage d* when found. *Stages a–d* rest upon observations made upon the youngest lot collected ; *e–h* are consecutive stages of the oldest lot. As I have the dates of the stages figured, the record is complete, except for the time between *d–e*, which may be from 24–48 hours. The record, compiled from my notes, is as follows :—

Stages a and b. The youngest eggs collected May 27, at 10 A.M., showed no visible traces of external folds. Their appearance 24 hours afterward (10 A.M., May 28) is represented in Figs. 5–9. The development was somewhat uneven, and *Stages a* and *b* were selected as the extremes.

Stage c. These were drawn from the same lot as *a* and *b*, six hours afterward, May 28, 4.10 P.M. (Figs. 10, 11.)

Stage d. Killed May 29, 12.20 M. (Figs. 12, 13.)

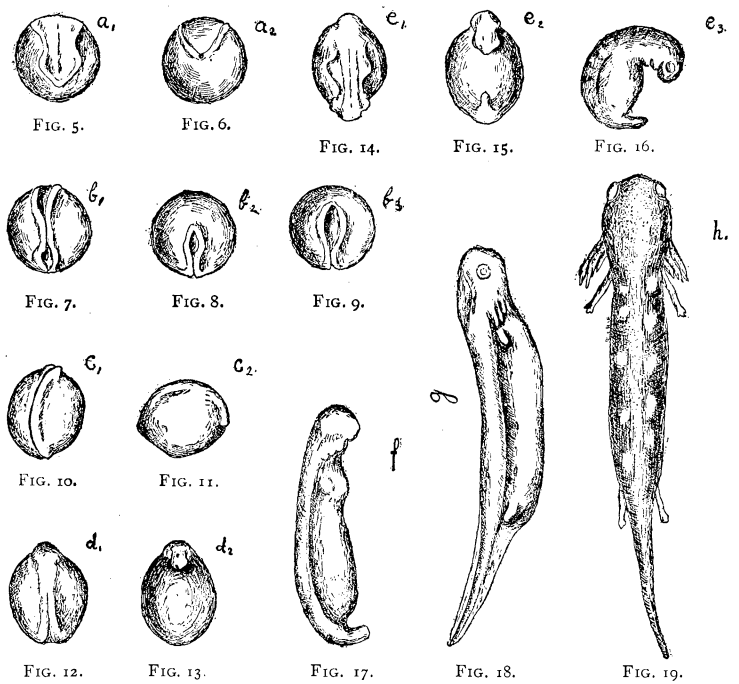
Stage e. These are from another and more advanced batch of eggs. All the other stages are taken from this lot.

The specimens of *Stage e*, as figured here (Figs. 14–16), were killed May 28, 4 P.M. The time it takes *Stage d* to reach the

development shown by *e*, I cannot tell, but suppose it to be 24–48 hours.

Stage f, June 1. (Fig. 17.) Embryos move in eggs when disturbed.

Stage g, June 6. (Fig. 18.) For this stage I have the following memorandum: "When taken out of egg membranes, swim about in watch crystal very vigorously for a few seconds and



FIGS. 5–19. — Developmental Stages of *Spelerpes bilineatus*.

repeat this each time when touched. Dorsal surfaces show pigment, light grayish appearance. Under lens, minutely mottled with pale gray dots (pigment cells), 6–7 little squarish areas left unpigmented in double row along back. These are to be the characteristic light spots of the larvæ." 5–7 days after reaching this stage the larvæ hatched. In the first case observed, June 11, the eggs broke when extracted from the water and liberated the larvæ. A note as follows: "It had to be *caught* with the little net; it swam about rapidly from one

side of the tank to the other and *avoided* the net. Could not be caught with a watch crystal. Movement, avoiding the net, etc., as in older larvæ." On June 13 the rest hatched.

Stage h. (Fig. 19.) Killed June 16, three days after hatching, 12.5 mm. long.

Development of Desmognathus. — Although I have fewer stages here to record, I can be more certain with the time-ratios between the stages, since all the observations were made upon a single batch of eggs, the ones described above, found

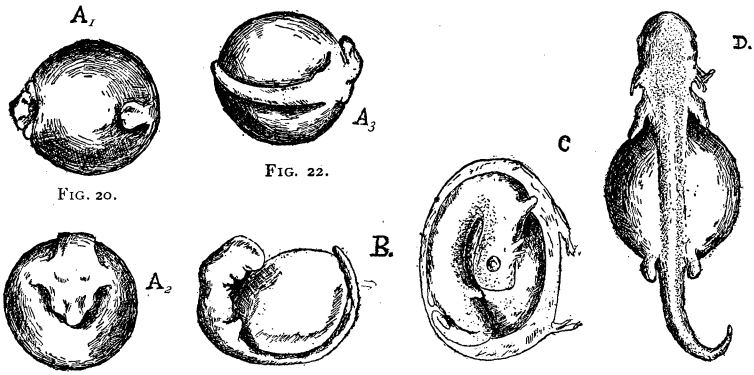


FIG. 20. FIG. 22. FIG. 21. FIG. 23. FIG. 24. FIG. 25.

FIGS. 20–25. — Developmental stages of *Desmognathus fusca*. In the above series the stages are represented by letters, small letters for *Spelerpes* and capitals for *Desmognathus*. The stages in the two series do not correspond. Different views of the same stage are designated by numbers attached to the letter. *All the figures are magnified five times.*

June 1, and probably laid the night or the day previous. My observations cover but four stages, as figured here, and the dates of the stages are as follows:

Stage A (Figs. 20–22), June 11.
Stage B (Fig. 23), June 14.
Stage C (Fig. 24), June 18.
Stage D (Fig. 25), June 21.

The pigmentation which was distinctly noticeable in *Stage C* had by June 24 distributed itself in the characteristic pattern, leaving little unpigmented squares in the manner described for *Spelerpes*. I killed the last embryo June 30, at which date the

specimen, although still in the egg, and leaving a large yolk-sac, was in other respects a fully developed larva. The pigmentation was complete, the external gills fully developed, and the feet had the full number of distinct toes (4 anteriorly, 5 posteriorly).

Larvæ of Desmognathus fusca. — From the suggestions of the previous paragraph, it becomes probable that the larva of *Desmognathus* remains in the egg until very well developed. My oldest embryo, taken from the egg June 30, is 13 mm. in length, still possessing so large a yolk-mass that it was evidently intended to remain in the egg for a much longer time.

I have taken *Desmognathus* larvæ only during the months of August–October, and these vary from 20–30 mm. in length, with external gills much reduced.

During fall and early winter the smallest adults are found 35–40 mm. in length, and differing from the largest larvæ mainly in the absence of the external gills.

Summing up the evidence, it becomes probable that the larvæ of *Desmognathus* remain in the egg until nearly adult, that they emerge from the egg in midsummer, that the gills, smaller at the time of hatching than at an earlier embryonic period, become gradually lost — a process which becomes complete during the late fall of the same year in which the eggs are laid. This history will readily explain the fact why the larval *Desmognathus*, perhaps the commoner of the two species considered, is so rarely met with. I have collected many hundreds of the larvæ of *S. bilineatus*, and a very few, not more than twenty in all, of the larvæ of *D. fusca*. In habits these larvæ resemble the adults. They avoid the deeper pools which abound in the larvæ of the other species, and lie where it is very shallow or in the wet sand, where they may find in places just water enough to cover them. When alarmed they run rather than swim, often abandoning the water, running with a series of quick jumps over the wet sand. COPE's only mention of this larva is so short and couched in such general words as to be applicable to either species. He says: "Its delicate larva may be observed darting rapidly from place to place, seeking concealment among mud and leaves." The color and marking

of this larva, as before mentioned, are identical with those of the larva of *S. bilineatus*, and are thus useless as a distinguishing test.

Larvæ of Spelerpes bilineatus. — The larvæ of *S. bilineatus* hatch early and continue for a long time in the larval state, probably 2–3 years.

COPE ('89) says: "It is one of those species whose metamorphoses are prolonged and which remains in the larval state until nearly grown." VERRILL ('62, '63) says of it, under the name of *D. fusca:* "The young become quite large before losing their gills." This description cannot apply to the genuine *D. fusca*, as has just been shown, and as the author has described in the same paper the eggs of *S. bilineatus*, the larvæ he found undoubtedly belonged to this latter species, concerning which the statement is an accurate one. The growth must be exceedingly slow and dependent upon the fortune of the individual in securing prey. I have caught all stages from 16–52 mm. at all seasons of the year, and see no indication that those larvæ collected at any one time represent one, two, or three years of definite growth.

For the purpose of studying this point I went to Williamstown, Mass., in September, 1896, collected 90 larvæ, and measured and tabulated each.[1] The result of this is shown graphically in Fig. 26, in which the ordinates represent the total lengths in millimeters, and the abscissas the number found. The results seem to show, in general, merely a decrease in numbers as the animal gets larger, which was to be expected.

There are gaps in one or two places, indicating sizes that I did not find, but these are by no means wide enough to represent a year's growth. 52 mm. represents about the limit of size reached by the larvæ under the most favorable circumstances. I have found adults a little smaller than this.

Differentiation of the Larvæ. — The fact that the larvæ of *S. bilineatus* are exceedingly common, while those of *D. fusca* are rare, renders it *a priori* probable that a given larva belongs

[1] I was materially assisted in the collection of these larvæ by my good friend, the late Dr. James I. Peck, whose kindness I most pleasantly remember in this connection.

to the former species. This may become a certainty if the larva be above 35 mm. in total length. At about 20 mm. the larvæ of *D. fusca* have very small external gills, and the tail fin is obsolescent; while larvæ of *S. bilineatus* of the same size have very apparent external gills and a very broad tail fin, ending obtusely. In general, the larva of *D. fusca* is at all stages suggestive of maturity, while that of *S. bilineatus* is larval and piscine in its general appearance. The former resembles *Amblystoma* in shape, the latter *Necturus*. The former has a

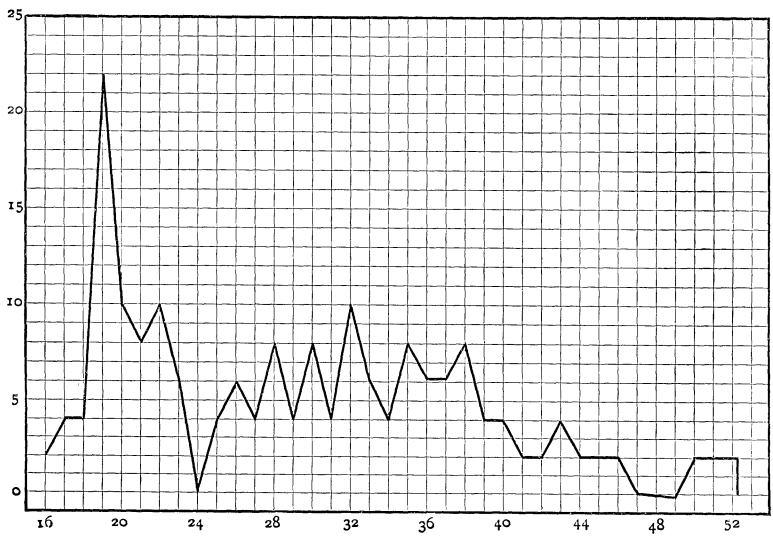


FIG. 26. — Curve showing frequency of the larva of *S. bilineatus* at its different stages.

short head, rounded above, shows well-marked costal folds, has robust limbs and a narrow tail fin. The latter has a long flat head, obscure costal folds, and a very broad tail fin. A definite distinguishing characteristic does not seem to exist, but there are so many general distinctions that a person who has once studied and compared the two will find no difficulty in identifying each species at any stage.

Method of Rearing in Confinement. — The adults of both species, because of their peculiarities in respiration and the consequent necessity of keeping their skin moist, cannot be kept either in water or in a dry atmosphere, but may easily

be kept for months or years in an ordinary fernery where the atmosphere is constantly saturated with moisture. I have in my laboratory a large fernery or *terrarium*, about 2 × 3 feet square and 2 feet high. The bottom consists of a zinc tray, 8 inches deep and water-tight. The top and sides are of glass and the front side runs in a frame with weights, being thus capable of being raised and lowered like an ordinary window-sash. In the bottom of this there are about 6 inches of good garden soil, in which are planted ferns and other wood plants. The surface is partly covered with moss, and here and there are placed several stones, the size of one's fist, and a few pieces of rotten stump, arranged so as to give shelter to the adults. In one corner a crystallizing dish is sunk to the level of the soil. This is filled with water and the bottom covered with a little fine sand. Some duckweed, or Salvinia, may be placed upon the surface, and a few small stones should be put in a dish. At the beginning of the season, after arranging everything as above, enough water is poured in to drench the soil, and the sunken dish is filled. After this the *terrarium* is self-regulating. The water that evaporates is re-precipitated as moisture, and the total loss from the little pond in the corner is so slight that it needs replenishing not oftener than once in six months. If the *terrarium* is to support many animals, it is better to place a few earthworms, myriapods, etc., in it; and if the pond is designed for the rearing of larvæ, supplies of Entomostraca and a little Spirogyra to feed them with should be occasionally introduced. I have tried placing tiny bits of meat in prominent places, but they merely mould and have to be removed. I have kept as many as 20–30 adults and a dozen larvæ in my *terrarium* during an entire college year, and several times, on clearing it out in the fall after the summer vacation, I have found alive and in good condition adults which I had been unable to find in the spring, when I intend always to remove the animals. It seems most probable that these salamanders find enough to eat among the worms and insects introduced with the earth and plants, as they always appear in perfectly normal condition and contrast very forcibly with *Diemyotylus*, which grows thin and often starves to death when placed under

the same conditions. An examination of stomachs would, of course, settle this point; but I do not happen to have on hand at present any specimens which are known to have been kept for a long time in this manner.

Advantages as Laboratory Animals. — The advantage suggested in the previous paragraph is an important one, being animals that may be *easily kept in the laboratory during the winter without feeding or other attention.* To collect them from the *terrarium*, lift up the stones exactly as when in the field, or else wait until 9 or 10 P.M., and bring a light suddenly upon them. They are nocturnal and at such times forsake their concealment and crawl about over the glass sides and roof.

A second great advantage is that they *may be collected out of doors all the year round, except during the time of deep snow.* I have collected them with ease here in December and in March, thus leaving an interval of not more than 8–10 weeks during which they cannot readily be obtained. The eggs are peculiarly adapted to all sorts of experimentation; they lack the black pigment of the frog's egg, and thus give better results in staining. As their development is later in the year, they may be obtained after the eggs of frogs and toads have disappeared. The eggs of *S. bilineatus* develop readily when removed from the rock on which they are laid, if they are placed upon sand in a dish of water into which fresh water is constantly being introduced through a small pipe or glass tube. Those of *D. fusca* develop in the *terrarium*, and may be removed singly from the mass without disturbing the parent. It is highly probable that a mass of *Desmognathus* eggs would develop equally well when removed from the parent, if kept in the *terrarium* under the usual conditions; but I have not yet had an opportunity to test this, and it is at least possible that necessary moisture and even warmth may be derived from the body of parent.

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